

Field evaluation of drought response in small-grain cereals

R.E. Sojka

Coastal Plains Soil and Water Conservation Research Center, US Department of Agriculture, Agricultural Research Service, Florence, SC 29502, USA

Introduction

Those who have developed selection criteria for drought resistance in small grains and those responsible for evaluating the expression of drought resistance in small grains are very frequently not the small-grain breeder. As a result, there exists a conflicting multiplicity of thought on three vital aspects of this topic, namely: (1) what is drought resistance; (2) how does one breed for drought resistance, and (3) how does one test for drought resistance in the cultivars released? These are not simple questions (Eslick and Hockett, 1974). Furthermore, nearly all the agricultural disciplines, in addition to plant breeding itself, have their own definite ideas about the answers. Finally, these ideas frequently conflict at one or more levels. The result is a great diversity of thought—some of which reflects discordant and, at times, mutually exclusive concepts.

It is noteworthy that in the pursuit of drought resistance, much of the experimental activity has been directed along two broad approaches. These approaches might be labelled 'environmentalistic' (e.g. the approaches of Hurd (1974) and Retiz (1974)) and 'plant-engineering' (e.g. guided by such works as De Michele and Sharpe (1974), Lemeur and Blad (1974), Milthorpe and Moorby (1974) and Shawcroft *et al.* (1974)). The 'environmentalistic' approach is frequently used by agronomists, soil scientists, whole-plant physiologists, for example, and the 'plant-engineering' approach is often used by traditional plant breeders themselves. whole-plant physiologists, plant anatomists, biochemically orientated plant physiologists, etc. Disciplines active in either class are not rigidly exclusive. The approach taken in each instance, however, is substantially different. The environmentalistic school relies on plant performance in reaction to quantifiable levels of stress as the best determiner of drought resistance. Quantifiable traits associated with each entry in a germplasm collection are noted, and the entry's performance is evaluated over a range of stress. This provides the empirical basis for the identification of those traits likely to contribute to drought resistance in the breeding process. The plant-engineering school begins with a preconceived concept or ideotype of what traits a drought-resistant cultivar should, in theory, possess, such as awns (Grundbacher, 1963; Reitz, 1974), leaf erectness (Donald, 1968), heavy cuticular wax production (Hull, Wright and Bleckmann, 1978; Johnson.

Richards and Turner, 1983), deep prolific roots (Hurd, 1974), etc. Germplasm is selected and crossed to produce a cultivar as close to the ideotype as possible.

Several studies have underscored the inadequacy of rapid laboratory screening techniques or individual drought-resistance traits to acceptably predict whole-plant performance effects on yield under stress (Blum, 1979, 1983; Sammons, Peters and Hymowitz, 1980; Nass and Sterling, 1981). In the end, therefore, both the environmentalists and plant engineers must field-test the 'new' cultivars they have produced that they believe to be drought resistant. Ultimately, release of drought-resistant cereals depends upon establishment of acceptable criteria for a common definition of drought resistance. Regardless of the philosophy under which a cultivar has been bred, only an empirical environmental test of field performance can provide conclusive proof of the cultivar's drought resistance. How does the new cultivar perform in response to drought stress in the field? Although the latter point may seem obvious, how one quantifies and interprets 'performance in response to drought stress in the field' is itself the source of significant philosophical disagreement. The environmentalist must solve the dilemma of what is drought resistance both at the beginning and the end of his quest, by definition. In reality, however, even the plant engineer must have his definition of drought resistance in mind at the outset, because it will dictate the nature of the ideotype he designs and attempts to breed.

It is with concern for achieving relevancy, accuracy, and the greatest possible precision in the 'final' determination of drought resistance that the following review is written. Both the environmentalists' and the plant engineers' approaches are accepted as equally valid. The sole caveat assumed is recognition of the compelling need to define and evaluate drought resistance in terms *both* of the cultivar's intrinsic, non-stressed yield potential (its success at coping with all factors affecting it except drought), and of its yield reduction as a function of some quantifiable measure of stress severity. In other words, aspects (1) and (3) in the introductory paragraph are addressed, leaving (2) to the inclination of the reader, but recognizing that ultimately (1) and (3) demand an environmentalistic approach.

Defining drought resistance

Some researchers have accepted as drought resistance itself, certain quantifiable characteristics that are merely traits contributing to drought resistance. An example might be the declaration that a cultivar is drought resistant because it maintains a high plant-water potential when exposed to extremely low soil-water potentials. Of itself, the relationship of plant-water potential to soil-water potential is a trait that may or may not contribute to drought resistance. In any plant, the definition of drought resistance must be linked to survivability. In annuals, such as the cereal grains, the ultimate measure of survivability is production of viable seed. Conveniently for agriculturalists, the production of viable seed is essentially synonymous with yield.

Indexing yield to some quantifiable measure of stress severity, therefore, it is the only means of quantitatively evaluating relative drought resistance in a large collection of cultivars. This approach must be taken, since cultivars cannot be bred for drought resistance alone, but rather must be capable of performing acceptably in response to all the local factors affecting yield (e.g. temperature, daylength, fertility, pests, pathogens, and cultural peculiarities) as well as drought.

Drought resistance may in some instances need to be categorized according to the growth stage in which it occurs (Begg and Turner, 1976), e.g. early (preanthesis), midseason (flowering), late season (grain fill) or intermittent. When drought is preanthesis, midseason, or intermittent, stress recovery may be equally or more commercially relevant than is resistance to an uninterrupted terminal drought (Bauer, 1972; Loresto, Chang and Tagumpay, 1976; Schmidt, 1983). Passioura (1982) described two modes of plant response that are relevant when considering the nature of the drought episode. He called these modes 'conservative' and 'prodigal'. Conservative plants react incrementally to stress, gradually closing stomata as soil water is depleted and slowing water consumption and growth. Prodigal plants operate in an on-off fashion, consuming water at a nearly constant rate, with stomata wide open, until a critical depletion level triggers stomatal closure. The plants then enter a state of reduced growth and metabolic activity until the water supply is replenished. In prolonged or unbroken terminal drought, the conservative response is better. In short-term or intermittent drought episodes, the prodigal response results in less reduction of yield potential, unless, of course, the episode exceeds the environmental limits of the prodigal plant's survivability, or unless a protracted suspension of activity occurs at a critical period, such as pollination or grain filling. The latter risk assumes greater importance in determinate plants (Salter and Goode, 1967). Work with various crops other than small grains reviewed by Begg and Turner (1976) indicated that, in many instances, the prodigal response is capable of fully compensating for brief periods of stress. The mechanisms that allow the accelerated growth and development needed for a stressed crop to 'catch up' to its non-stressed counterpart are not well understood and are the source of great speculation.

Water use efficiency (WUE) is inappropriately and all too frequently equated with, or used to assess, drought resistance (Hsiao and Acevedo, 1974; Reitz, 1974) where WUE is defined as grain yield per unit water consumed. In most instances, apparent changes in WUE are merely a reflection of optimal yield potential, and/or differences in cultural practices or cultivar characteristics that affect plant vigor, weed competition, depth of water extraction, and attainment and duration of ground cover by the canopy (Pendleton, 1966; Viets, 1966; Fischer and Wall, 1976). Fischer and Turner (1978) point out that WUE is best defined as dry matter produced per unit transpiration (not evapotranspiration). They further explain that enhanced WUEs can usually be traced back to increasing transpiration as a fraction of evapotranspiration, resulting either from greater soil extraction, greater canopy coverage (which reduces soil evaporation), or from increases in harvest index. Where WUE is equated with drought resistance, serious misinterpretations of findings can result if the effect of the ontogeny of the cultivars compared is not considered. Onset of drought after flowering will, for example, reduce harvest index more than when the onset of drought occurs before flowering (reducing vegetative growth).

Levitt (1972) introduced a unique concept for dealing with plant stresses. To give plant scientists a more precise nomenclature for dealing with the concept of environmental stress, he transferred to biology the language of mechanics. He defined biological stress as any environmental factor capable of inducing a potentially injurious (plastic or irreversible, i.e. non-elastic) strain. Levitt recognized certain inherent differences between biological systems and inanimate mechanical systems. Duration of stress in biological systems can positively or negatively affect the magnitude of strain. Over time, an organism can deteriorate,

adapt, or otherwise change due to aging. For example, Reicosky, Campbell and Doty (1975) found that resistances to water flow through the plant may change with age, altering the effective availability of soil water at a given water potential gradient. Even after strain has occurred, an organism has the capacity to repair (heal) the injury. Therefore, in the truest sense, the irreversibility of strain must be qualified to mean partially irreversible, and/or irreversible over a finite time span.

In deriving a working definition of stress resistance, Levitt (1972) modified his physical analogy to explain what Precht, Christophersen and Hensel (1955) and Precht (1967) had termed 'resistance adaptation' and 'capacity adaptation'. Levitt (1972) recognized that an organism's stress resistance could operate through one of two mechanisms: (1) by excluding or 'avoiding' the stress or (2) by surviving the injury, i.e. 'tolerating' the stress. Stress tolerance could in turn operate through one of two mechanisms: (1) although stress might not be avoided, the organism could have the ability to avoid strain (strain avoidance); or (2) once strained, the organism could have the ability to repair the strain (strain tolerance). He thus equated strain avoidance and strain tolerance with Precht's capacity adaptation and resistance adaptation, respectively.

In applying these principles to define drought resistance, Levitt (1972) conceptually recognized the need to interrelate an index of plant injury to an index of stress severity. He explained that drought resistance can be defined in terms of 'the water stress necessary to produce a specific plastic strain'. The choice of parameters used to quantify the level of stress and the intensity of strain are somewhat arbitrary. None the less, it is significant that Levitt frequently utilized water potentials and yield in explaining the concept.

A final point in discussing Levitt's nomenclature is that although he identifies numerous mechanisms which contribute to drought resistance (via a variety of evolved strategies), the specific mechanisms are only of importance in assessing relative drought resistance if they are tied to the measurement of stress severity. For example, assessment of drought resistance among cultivars could be confounded if the drought was an uninterrupted terminal drought and the cultivars being compared had widely divergent maturity dates. In this instance, if all cultivars were planted on the same date, the very early cultivars could begin to senesce before available soil water was significantly depleted. They would 'escape' drought and never actually be exposed to significant environmental stress. If yields were compared from such a study, yields from stressed, late cultivars, would be compared with yields of non-stressed, early cultivars, both from supposedly the same treatment. This is because in reality the early-maturing cultivar never experiences an equivalent amount of stress, regardless of how stress is quantified (transpiration deficit, plant-water potential, soil-water potential, etc.).

Even though earliness is a valid production strategy (MacKey, 1966, 1970; Derera, Marshall and Balaam, 1969; Ray *et al.*, 1974; Reitz, 1974), it should be recognized that a cultivar that escapes drought may do so even if it is the exact idotype of drought susceptibility! It may, in fact, have no drought resistance whatsoever if actually exposed to drought. It could, therefore, be quite counterproductive to identify such a cultivar as a source of drought resistance in a breeding program. In transferring its earliness, some other unrecognized negative traits could also be transferred. One strategy to reduce the likelihood of such experimental confounding is to delay planting of earlier cultivars, so that all cultivars in the test reached a fixed stage of development (e.g. anthesis or maturity) at the same time (Fischer and Maurer, 1978; Sojka, Stolzy and Fischer, 1981).

While earliness in cereals is frequently associated with reduced yield potential in the absence of stress, successful transference of the sole trait of earliness could enhance drought resistance in otherwise suitable cultivars.

Quantifying drought resistance

Defining the limits of drought resistance by 'the water stress necessary to produce a specific plastic strain' is intentionally vague with respect to the parameters and units employed to quantify water stress and plastic strain. Water stress must be tied either to a direct measurement of the environment or a closely integrated plant-environmental response, such as plant-water potential or leaf vapour pressure deficit (as defined by Burrows and Milthorpe, 1976). The single most relevant indicator of plastic strain in cereals is expressed through a reduction of grain yield. Total shoot production is important only if forage or bio-energy value of the straw is relevant. Only grain production will be considered in the following discussion.

Various specific approaches have been employed in the case of each parameter. Until recent years, the quantification of stress intensity and duration has been largely ignored. This is particularly disturbing, inasmuch as even in so-called non-stressed nurseries the levels of stress are probably underestimated in many instances. The contribution of spatial variability with respect to soil hydraulic properties, canopy geometry, border (and/or so-called 'clothesline') effects, etc., are seldom considered. Similarly, simple comparisons of absolute yields or even relative treatment yields when relying on standard statistical approaches (analysis of variance, LSD, Duncan's multiple range test, etc.) to discriminate differences in cultivar performance may be inadequate.

Some conceptually related approaches that begin to describe quantitatively the complex interaction of stress level and cultivar response have been described by several researchers (Finlay and Wilkinson, 1963; Allard and Bradshaw, 1964; Eberhart and Russell, 1966; Finlay, 1968; Grafius, 1971; Easton and Clements, 1973; Blum, Gozlam and Mayer, 1981; Sojka, Stolzy and Fischer, 1981; Fox and Rosielle, 1982; Blum, 1983; Jensen and Cavalieri, 1983). Each approach varies in complexity and statistical rigor. Eberhart and Russell (1966), for example, identified stress resistance by evaluating the statistical stability of cultivar yield across environments, where a stable variety was regarded as one with a regression coefficient (slope of the regression line) of 1.0 and with a mean square of deviation from the regression of zero. However, even the simpler techniques link quantitative field assessment of drought resistance to simultaneous characterization of stress severity and stress response.

Allard and Bradshaw (1964) and Easton and Clements (1973) used regression analysis to contrast overall population responses with individual cultivar response. Their work, which was an extension of concepts originally suggested by Haldane (1946), provided a relatively reliable method of quantifying stress severity in the absence of sophisticated instrumentation and simultaneously related stress severity to yield response for each increment of stress observed. The precision and, to a lesser extent, the accuracy of this technique are dependent upon the researcher's capacity to ensure that all other factors affecting the experiment are uniform across all varieties and stress treatments. In its simplest form, their approach compares an individual cultivar's response (dependent variable) with that of the mean linear

response of all entries in the trial (independent variable) for the desired trait (preferably yield—unless there is some other logical or compelling index of stress to be compared, e.g. plant-water potential, leaf vapour pressure deficit, stomatal conductance, canopy temperature, etc.). The regression line of the individual cultivar's response is then compared with the regression line of the total population. Numerous interpretations can be made.

Figure 7.1 presents a hypothetical example of such a plot. The conclusions drawn from such a representation are most reliable when the population examined is large and dominated by entries that are predominantly known to be well suited for local conditions. As stated earlier, only one source of stress is imposed on the experiment. The greater the number of stress increments, the more reliable one's interpretation of the data is likely to be.

In such an experiment, the separate response of most of the individual cultivars would appear linear and nearly indistinguishable from the 1:1 line. Only a few outlying responses would be obvious. If an outlying response were distinguished primarily by an intercept significantly different from the 1:1 line, but with a slope not significantly different from unity, the response is interpretable in terms of the cultivar's relative suitability to all factors in the local environment except the one intentionally varied. Line A in Figure 7.1 is such a response. In this case, the y

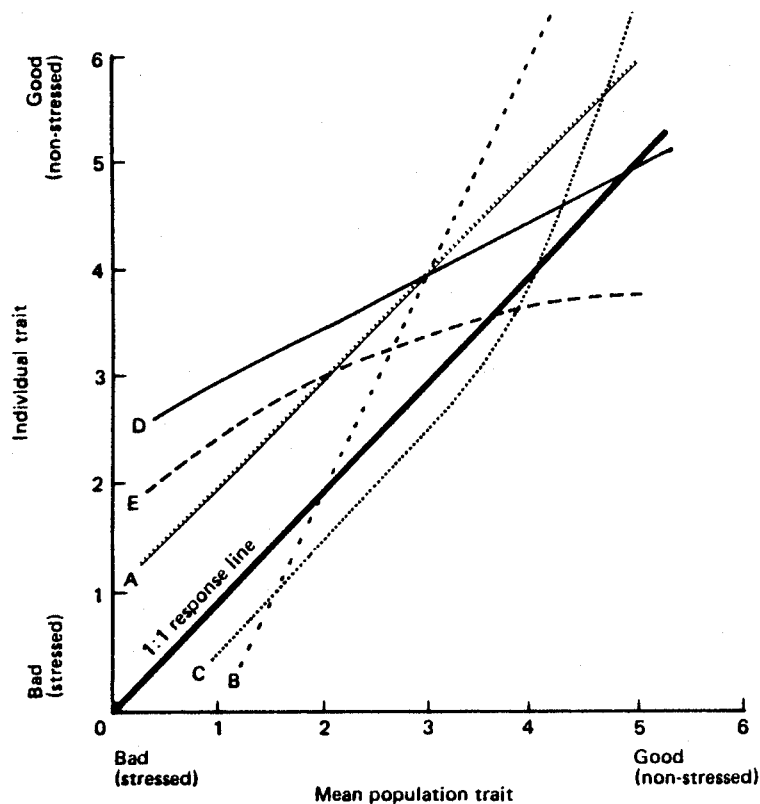


Figure 7.1 Determination of stress resistance of individuals through stability analysis with response regressions

intercept is greater than the 1:1 line, indicating outstanding suitability for local conditions (e.g. perhaps the cultivar has resistance to a local insect pest), but the parallel slope indicates that cultivar A responds identically to each increment of drought stress as the population mean. If line A were parallel to the 1:1 line, but had a smaller y intercept (was under the 1:1 line), it would indicate particular sensitivity to some local factor in the environment, but again, no difference in drought susceptibility. Before going to the next example, it might be worth pointing out that an analysis of this type makes use of the simple conceptual model proposed by Lewis and Christiansen (1981). They suggested that the interaction of genetic potential (g) and environment (e) to produce yield (y) could be expressed as the linear equation:

$$y = ge + a \quad \text{Eq. (7.1)}$$

where (a) is a constant (the intercept).

Line B represents the response of a cultivar sensitive to drought. In the case of B, the plot is linear over the stress range observed, with a slope greater than unity, indicating a greater susceptibility to each increment of stress than the population mean. The trait degrades uniformly over the range of stress observed. The evaluation of the stress susceptibility can be weighted either by the slope or the point at which B's yield falls below the population mean. In this example, B out-performs the population across all but the severest ranges of stress. The latter interpretation is more relevant in making a variety recommendation to the farmer than it is to identification of stress resistance for breeding. This is because in spite of a total genetic make-up resulting in excellent yield potential in the absence of stress, one or more traits (that may be heritable) are contributing to severe drought sensitivity when water availability is the only factor in the environment that is varied. In terms of *Equation 7.1*, the source of variation in performance (slope) is g , since e is the same for all varieties at each level of stress.

Line C is also an example of a drought-susceptible cultivar. It differs from B in its curvilinear shape, resulting from greater sensitivity (slope > 1.0) to drought stress in the first increments of stress encountered. At more severe levels of stress, cultivar C exhibits stress sensitivity similar to the population mean (slope approaches 1). Intuitively, drought response could not be expected to be truly linear as in *Equation 7.1* (although it may approach linearity over defined ranges of environmental stress). If the form of the equation were linear and if one used finite amounts of applied water to create the stress ranges, then deviations from the 1:1 line would have to be explained with positive intercepts in some cases at the zero water increment, or even more absurdly, negative yields would occur at times in the presence of applied water. In reality, yield would be expected to remain at zero until a critical amount of water had been applied, then increase rapidly with successive increments of applied water until reaching a linear phase, level off on a plateau of maximum yield expression, and then decline when soil water became excessive.

Line D represents what might be regarded as a nearly ideal drought-resistant response. In the non-stressed range, cultivar D matches the mean performance of the population. With each increment of stress, cultivar D exhibits a uniform, but more gradual degradation of the trait observed (a linear response with slope < 1.0). Line E is probably most like the drought-resistant cultivars that exist in reality (Knight, 1970; Schmidt, Johnson and Stroike, 1972; Rosielle and Hamblin, 1981; Sojka, Stolzy and Fischer, 1981). Some non-stressed yield potential is sacrificed

because of the presence of traits intended to stabilize yield during stress, preventing achievement of maximum yield potential (Fischer and Wall, 1976; Hanson and Nelsen, 1980; Schmidt, 1983). As stress becomes increasingly severe, however, the cultivar eventually displays the same sensitivity to stress as the overall population (slope approaches 1.0).

The hypothetical responses of cultivars C and E bear a strong resemblance to the actual responses of the two most significant outlying cultivars in a wheat (*Triticum*

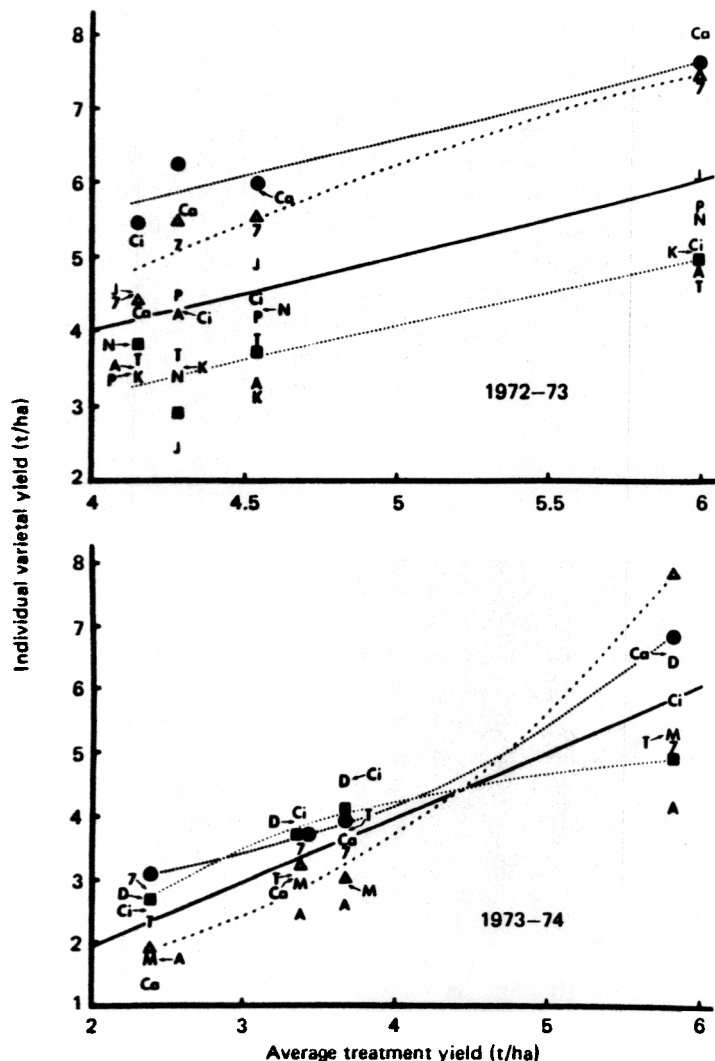


Figure 7.2 Best fit of individual cultivar yield as a function of mean cultivar yield for each treatment. The pooled response best fit and the 1 to 1 response line were statistically identical. Letter symbols A, Ca, Ci, D, J, K, M, N, P, T, and 7 represent cultivars Armadillo, Cajeme 71, Ciano 67, D67-3, Jori 69, Kloka, Maya II, Nainari 60, Pitic 62, T64-2W, and 7 Cerros, respectively. Each point is the mean of four replicates — pooled; ●—● Yecora 70; ■····■ Gabo; △----△ Cocorit 70. (Sojka, Stolzy and Fischer, 1981)

aestivum L. and *T. turgidum* L. var. *durum*) study conducted by Sojka, Stolzy and Fischer (1981) in the Sonoran Desert of Mexico (Figure 7.2). Thirteen and ten wheat genotypes were observed in the first and second years of the study, respectively. The genotypes were subjected to varying intensities of uninterrupted terminal drought.

In the first year of their study, one significant rainfall event disrupted the drought treatment and genotype yields responded primarily in the manner explained for the hypothetical cultivar A. Several high-yielding Mexican semi-dwarfs, Cajeme 71,

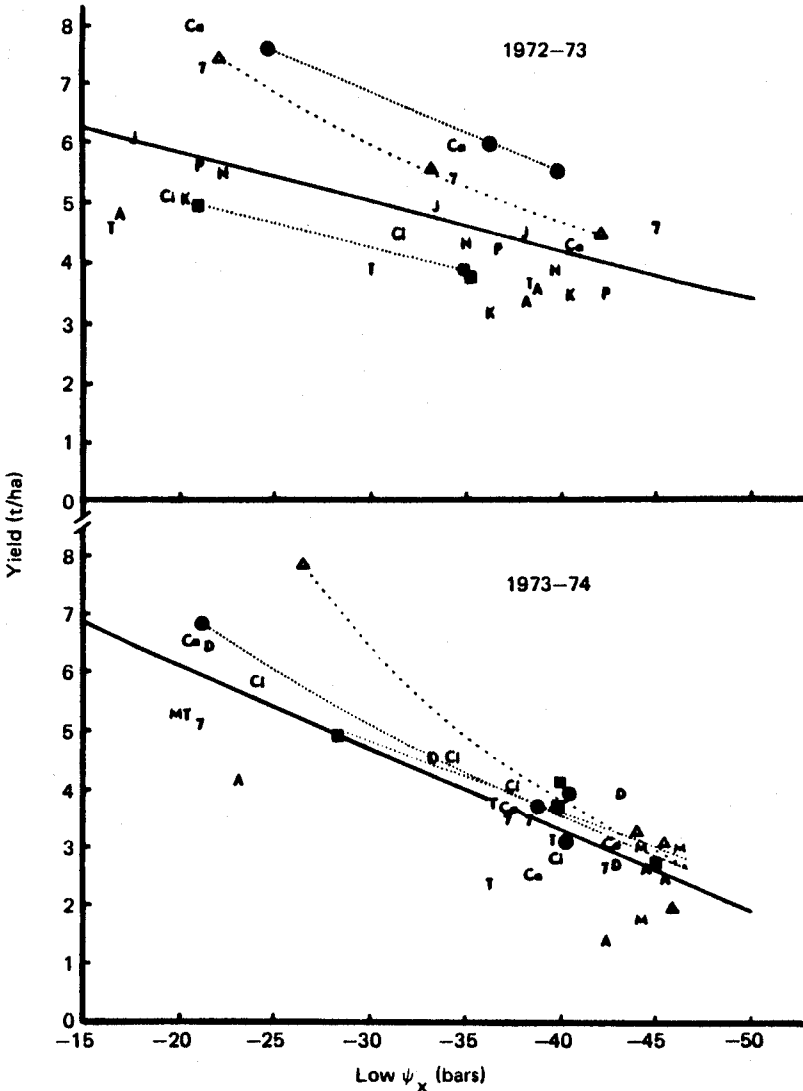


Figure 7.3 Yield as a function of lowest observed midday ψ_x . Mean r^2 for the best fit of each cultivar are 0.989 and 0.877 for the two seasons, respectively. Letter symbols A, Ca, Ci, D, J, K, M, N, P, T, and 7 are the same as those in Figure 7.2. Each point is the mean of four replicates — pooled; ● — ● Yecora 70; ■ — ■ Gabo; △ — △ Cocorit 71. (Sojka, Stolzy and Fischer, 1981)

Yecora 70, 7 Cerros 66, and Cocorit 71, showed superb local adaptation (elevated intercepts) with slopes that closely paralleled the population mean (similar drought sensitivity over the range of severity observed). Outlying responses below the population mean were primarily associated with non-adapted genotypes from outside Mexico.

In the second year of their study (Sojka, Stolzy and Fischer, 1981), substantially more severe stress occurred. No rain fell during the entire growing season. Yields of the least stressed treatments in the second year began in the yield range of the most severely stressed treatment of the first year. Response of the genotype Cocorit 71 was similar to that of the hypothetical cultivar C in *Figure 7.1* and response of the cultivars Gabo and T64-2W were very similar to that of the hypothetical cultivar E in *Figure 7.1*. The rapid advancement of computing capability in the 1980s now makes it possible easily to determine least squares best fits of such data to numerous curvilinear mathematical models, even with inexpensive microcomputers. Better correlations of non-linear models more accurately define the limits of drought sensitivity and resistance of the cultivars tested. Understanding these limits could aid in selection of the best source of resistance genes for a particular breeding effort.

Where appropriate instrumentation is available, an absolute index of severity can be used to characterize stress, such as plant-water potential, the ratio of actual evaporation to potential evapotranspiration, canopy temperature, the normalized plant-water stress index or other valid indicators of stress severity. In turn, yield responses can then be directly related to the desired environmental index. Sojka, Stolzy and Fischer (1981) obtained results using xylem pressure potentials (ψ_x) that were nearly identical to those using the yield comparisons described above. Stress resistance and tendency for pronounced curvilinear responses were identified in the same genotypes (*Figure 7.3*). Numerous combinations of environmental indices and yield expression were tried before settling on absolute yield and lowest observed ψ_x (e.g. mean ψ_x vs. % control yields), but all provided essentially identical results.

Choice of yield and environmental indices

General considerations

Deciding which parameters to use to quantify stress, or how specifically to express yield, is governed by numerous factors, not the least of which are the scientist's resources, previous research interests and experiences. In actuality, numerous choices exist which could all be defended with substantial scientific arguments. Nass and Sterling (1981) concluded that no one test alone can reliably determine overall response to drought in wheat and barley (*Hordeum vulgare*). They even suggested avoidance and tolerance should both be characterized for each cultivar tested. As stated several times already, however, the important consideration is to develop a function which allows accurate comparison of yields over definable increments of stress. Comparison of genotypes or cultivars in any way that does not carry through to this step may indicate the presence of traits suspected of contributing to drought resistance, but they do not conclusively establish that a particular entry is resistant.

Some approaches to trait identification

One can argue that screening for the presence of drought-resistant traits is just as important to a breeder as the final test of drought resistance. This is particularly true for large-scale breeding efforts where several thousand entries must be evaluated over a short time period. Few, if any, of the so-called rapid tests for drought resistance, however, have subsequently been evaluated extensively and conclusively in the field in any manner similar to that suggested in the previous section. Consequently, they may focus too much attention on identifying a selected trait without a true appreciation of its relative merit as applied to field performance.

A number of approaches used to screen for the presence of drought-resistant traits involve biochemical assays, other laboratory-intensive physiological analyses, or ultra-short-term shoot-growth evaluations (Salim, Todd and Stutte, 1969; Dedio, Stewart and Green, 1976; Johnson and Brown, 1977; Ashraf and Abu-Shakra, 1978; Johnson and Asay, 1978; O'Toole, Aquino and Alluri, 1978; Sammons, Peters and Hymowitz, 1978, 1979; El-Beltagy and Hall, 1979; Blum, Sinmena and Ziv, 1980). Townley-Smith and Hurd (1979), Sullivan and Eastin (1974), Hanson and Nelsen (1980), and Turner and Begg (1981), reviewed numerous non-field tests for the presence of drought-resistant traits. These procedures are both beyond the scope of this chapter and largely outside the expertise of the author. A number of approaches developed in the greenhouse, in the growth chamber, and in the field, however, are worth discussion with reference to their field applicability.

GENETIC EXPRESSION

From the philosophy outlined to this point, it is already clear that grain yield (wt/area) as a function of stress severity is the preferred index of plant productivity under drought. This should not be interpreted as implying that there are no other morphological or anatomical parameters worth quantifying as functions of water stress. Various relationships of this nature provide useful assays for the presence of drought-resistant traits. Indeed, creative thinking in this phase of drought testing could help to guide the selection process by providing relevant and innovative insights which until now have not been recognized. The following discussion cites some previously reported applications and gives an example of how the concept might be extended.

There have been a relatively limited number of reports that describe potentially heritable traits as functions of quantified levels of water stress. One interesting area has been in the study of cuticular wax contribution to drought resistance. Dubé *et al.* (1975) related transpiration rate in the dark to leaf-water potential for two corn (*Zea mays* L.) hybrids to determine relative differences in leaf-cuticular resistance. They also observed dark respiration rate as a function of leaf-water potential. Cuticular resistances were significantly different between hybrids, whereas dark respiration rate was not. By mathematically treating the cutin matrix and cuticular waxes of three horticultural species as two resistances acting in series, Schönherr (1976) found that the cuticular waxes completely determined the water permeability of the cuticles. Furthermore, extraction of the cuticular waxes increased cuticle-membrane permeability by a factor of 300–500. Ebercrom, Blum and Jordan (1977) developed a rapid colorimetric method of quantifying cuticular

wax content in sorghum (*Sorghum bicolor* L. Moench), allowing screening of large numbers of selections over a range of stress. Bengtson, Larsson and Liljenberg (1978) found that when six oat (*Avena sativa* L.) cultivars were stressed, the greatest reduction in epicuticular transpiration occurred in the cultivar that responded with the greatest production of epicuticular wax. They also observed that the chemical components of the wax changed with stress severity, and that the nature of the changes in composition differed among varieties. Douglas, Richards and Turner (1983) found similar cuticular-wax build-up in near-isogenic lines of durum wheat (*T. turgidum* L. var. durum) and common wheat (*T. aestivum* L.) in response to stress; however, they observed no association of water relations with wax content. Isolines with waxier cuticles produced significantly higher yields in the two least severe of three stress ranges, but were not different at the most severe level of stress. Cuticular wax accumulation under stress has been reported in various species by a number of others including Wright and Dobrenz (1973), Baker (1974), Giese (1975), Hamilton (1975), Hunt, Holloway and Baker (1976), Van Volkenburgh and Davies (1977) and Hull, Wright and Bleckmann (1978). In many of the above, differences in the ultrastructure of the wax accumulations were also found to be affected by environmental factors, and it has been suggested that the nature of the ultrastructure as well as wax amount impacts the effectiveness of cuticular wax in inducing drought resistance.

Relatively little attention has been paid to improving pollen-related phenomena as they affect drought resistance in small grains. Khan, Heyne and Arp (1973) reported that seed set and yield patterns were directly related to pollination, and that in turn, pollination was significantly correlated with yield. It seems highly probable that quantifying pollen-related stability parameters with environmental indices and similar characterization of pollinating floral organs could contribute significantly to drought resistance, particularly when drought occurs before or during anthesis.

As stomata are directly involved in regulating transpiration losses, they often figure prominently in the architecture of drought-resistant ideotypes. Not as much attention, however, has been paid to actual stomatal characterization as to indirect indicators of stomatal response to stress such as leaf diffusive resistance (R_s), and its reciprocal, leaf conductance, etc. (Schmidt, 1983). Much of the discussion of stomata in this paper will follow in the next section, where R_s is addressed as an index of stress severity. It is difficult to separate the relative contribution of actual stomatal characteristics to observed R_s values from the effects of rooting patterns, leaf angle, xylem resistance, etc. Therefore, it seems more appropriate to regard R_s as an integrated environmental indicator.

Stomatal anatomy, physiology and function have been extensively reviewed in recent years (Cowan, 1977; Jones, 1977a; Körner, Scheel and Bauer, 1979; Raschke, 1979; Jarvis and Mansfield, 1981; Meidner, 1981; Farquhar and Sharkey, 1982; Kramer, 1983). A number of direct observations of stomatal characteristics (e.g. size and frequency) have been made, but there seems to be an inconsistent relationship between morphology and drought resistance (Muenscher, 1915; Miller, 1938; Freeland, 1948; Hesketh, 1963; Izahs and Wallace, 1967; Dobrenz *et al.*, 1969; Miskin and Rasmusson, 1970; Heichel, 1971b; Miskin, Rasmusson and Moss, 1972; Meyer *et al.*, 1973; Ray *et al.*, 1974; Walton, 1974), even though their physical characteristics are readily heritable (Heichel, 1971a; Wilson, 1971; Liang *et al.*, 1975; Tan and Dunn, 1975, 1976; Tan, Tan and Walton, 1976; Teare, Peterson and Law, 1971). As Jones (1977a) concluded, it appears that the

immediate potential for increasing drought resistance in cereals through manipulation of these traits is probably limited.

Leaf rolling is another physical trait that has potential for controlling R_s in cereals. Various reports of leaf rolling have been made by researchers comparing drought resistance among cultivars (Oppenheimer, 1960; Parker, 1968; Sojka, 1974; Begg and Turner, 1976; Sojka, Stolzy and Fischer, 1981; Schmidt, 1983). Although cereal grains are amphistomatal, they generally have greater stomatal densities and lower R_s on adaxial (upper) leaf surfaces. When complete rolling or curling occurs, the adaxial surface becomes enclosed and the abaxial surface, with lower stomatal density and higher R_s , is the only surface that remains exposed to the atmosphere. At the same time, the effective transpiring leaf area is halved. In many instances, rolling is also accompanied by an increased erectness of the leaves. Describing the behaviour of some stressed cultivars, Sojka, Stolzy and Fischer (1981) wrote 'with severe stress, flag leaves curl in soda-straw fashion and become nearly vertical'. O'Toole and Cruz (1979, 1980) examined this phenomenon in some detail in rice (*Oryza sativa* L.) and found that relative transpiration was reduced significantly with leaf rolling, especially as wind velocities increased. Furthermore, they associated leaf rolling with maintenance of elevated ψ_x through elevation of the effective R_s .

Intuitively, the plant characteristic most immediately implicated in the search for traits contributing to drought resistance has been plant-root geometry (Burton, 1959; Derera, Marshall and Balaam, 1969; Moss, Woolley and Stone, 1974). In spite of this, few 'breakthroughs' have emerged for plant breeding from root research. This is due to the difficulty of assessing root structure and function *in situ* and *in vivo*. In addition, observations of root characteristics in artificially constructed environments are notoriously suspect. Even if *in situ* observations could be made conveniently in the field, the problem would be compounded by the numerous soil physical and chemical factors that easily and drastically influence genetic expression of root habit. The monumentally challenging problem of root characterization has recently been excellently reviewed by Böhm (1979) and other comprehensive aspects have been previously reviewed by Whittington (1969), Carson (1974), Torrey and Clarkson (1975), and Bowling (1976).

With little exception it has been found that length of active roots per unit soil volume as a function of depth, and depth of penetration of the active root system, are the two root characteristics that most significantly affect drought resistance in cereals. Root length per unit soil volume affects the resistance to water entry into the plant, and depth of exploration substantially defines the volume of available stored soil water that can be extracted by a crop at a given site. The best single case-study of cereal breeding for enhanced rooting characteristics is chronicled by the success story of the Swift Current breeding effort (Hurd, 1974). Significantly, this is one of the few documented, economically successful efforts on record for release of new cultivars bred specifically for drought resistance.

Using stability analysis to evaluate the responses of yield components to stress appears to hold great promise. Fischer and his co-workers have been the most prolific workers in this arena. In a series of three papers (Fischer and Maurer, 1978; Fischer and Sanchez, 1979; Fischer and Wood, 1979), they explored the interaction of phenotype and environment in great detail in an extensive series of cereal trials comparing a score or more of entries over several years of observation. Among the parameters characterized were total dry matter, harvest index, kernels/m², kernel weight, kernel height, kernels/spike, spikes/m², cuticular wax, duration of grain

filling, green ground cover, and others. In addition to the thorough analysis of growth parameters, several indices of stress severity were used and several indices of, and predictive functions for, drought response were devised and evaluated. The reader is referred to the original publications for details. The work of Sojka, Stolzy and Fischer (1979, 1981), discussed earlier and in the following section, was conducted in conjunction with, and as a small part of, the overall CIMMYT physiology program with Fischer and his co-workers. Application of analyses

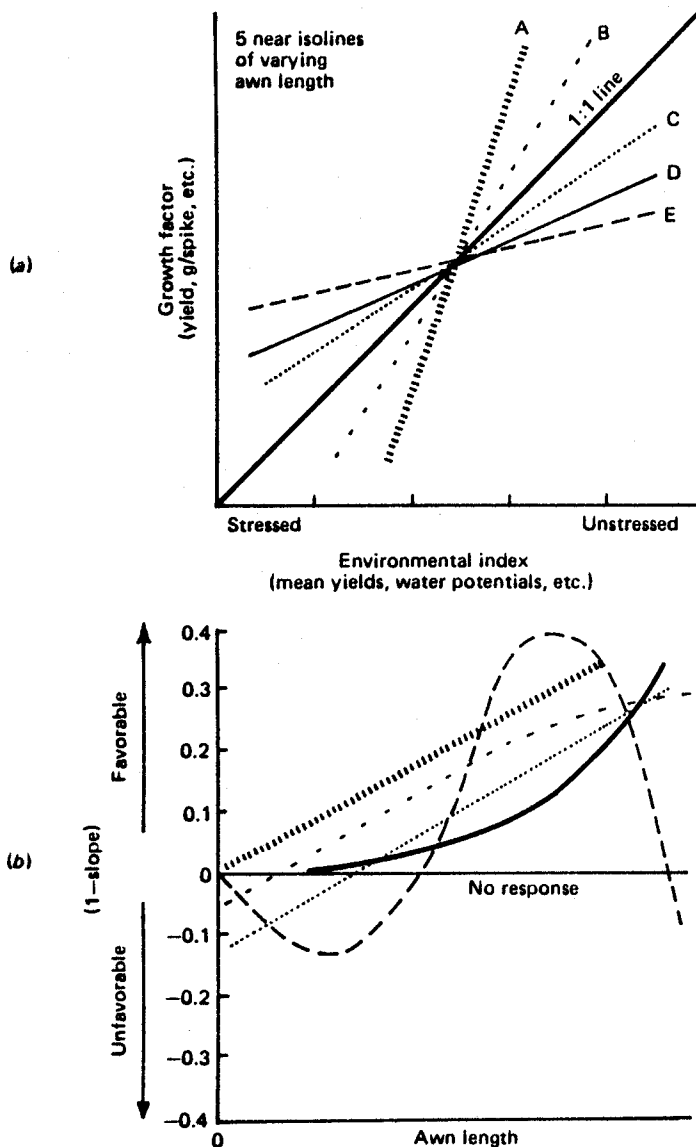


Figure 7.4 Use of stability analysis with response regression to quantify contribution of one trait to stress resistance (for explanation see text)

similar to those described in *Figure 7.3* were also employed with interesting results for various yield components by Fischer (1973), Fischer, Lindt and Glave (1977), and Blum, Gozlan and Mayer (1981). Keim and Kronstad (1981) related yield components to osmotic potential in wheat. In another paper, Grafius (1971) used stability parameters to describe yield component responses to stress and suggested the use of iso-stress lines to relate the plant response to quantifiable increments of stress.

As cited earlier, awns have been associated with drought resistance in cereals. In addition, Suneson, Boyles and Fifield (1948) and Atkins and Norris (1955) suggested that awns favored increased yield potential in general, except where collection of water in the awns and increased wind resistance of awns predisposed the cultivars to lodging during storms. Awn characterization provides a good example of how stability analysis might be extended to quantify the contribution of awns to drought resistance. What is the quantitative relationship of awns to drought resistance? Is drought resistance enhanced linearly or otherwise by the amount of awns per spike? Do all awned cultivars respond in the same manner?

If one were to stress several isolines (A–E in *Figure 7.4a*) that differed only in their length of awns, or alternatively, if one stressed a single awned cultivar and trimmed the awns to several increments of awn length, a yield stability analysis of the type explained in *Figure 7.1* could be conducted. The results might be plotted as shown in *Figure 7.4a* (for simplicity, linearity is assumed). Upon determining the slope of each response line, one minus that slope can be plotted against awn length to assess quantitatively the effect of awn length on drought response. Various possible responses are plotted in *Figure 7.4b*. The same technique could be used to assess the effect of numerous other anatomical or morphological characteristics such as tillers per plant (or per m^2), spikelets per spike, root length, stomatal number per cm^2 of leaf, flag leaf angle, g cuticular wax per m^2 of leaf, etc. Where stress response was suspected to vary according to timing of stress and for stress relief, separate analysis could be tailored to each probable scenario. The visual assessment of the response could be made more compact by presenting yield, environmental index, and character quantity on a single surface response. The polynomial function describing such a response surface would be a valuable tool in designing the optimal plant ideotype for a specific environment.

QUANTIFYING STRESS SEVERITY

Considerably more progress has been made in the past decade in our understanding of the physics and physiology of stress than in the genetics of stress resistance. The following discussion is intended to review some of the applications of stress measurements in cultivar comparisons.

Probably the three most common field measurements of plant-water stress are ψ_x , R_s and osmotic potential (ψ_π). Psychrometric measurement of total plant-water potential (ψ_p) has not been very useful in comparing varieties in the field because the measurements are tedious, easily confounded by instrument instability arising from such factors as temperature fluctuation, too slow in set-up and response time, and too expensive to attack from a multiple instrument approach. A new technology with great promise for future work is infra-red sensing of canopy temperature (T_c). Infra-red temperature sensing will be discussed in greater detail below with vapor pressure deficit (VPD), and leaf vapor pressure deficit (LVPD). Turgor pressure or relative turgidity comparisons of numerous

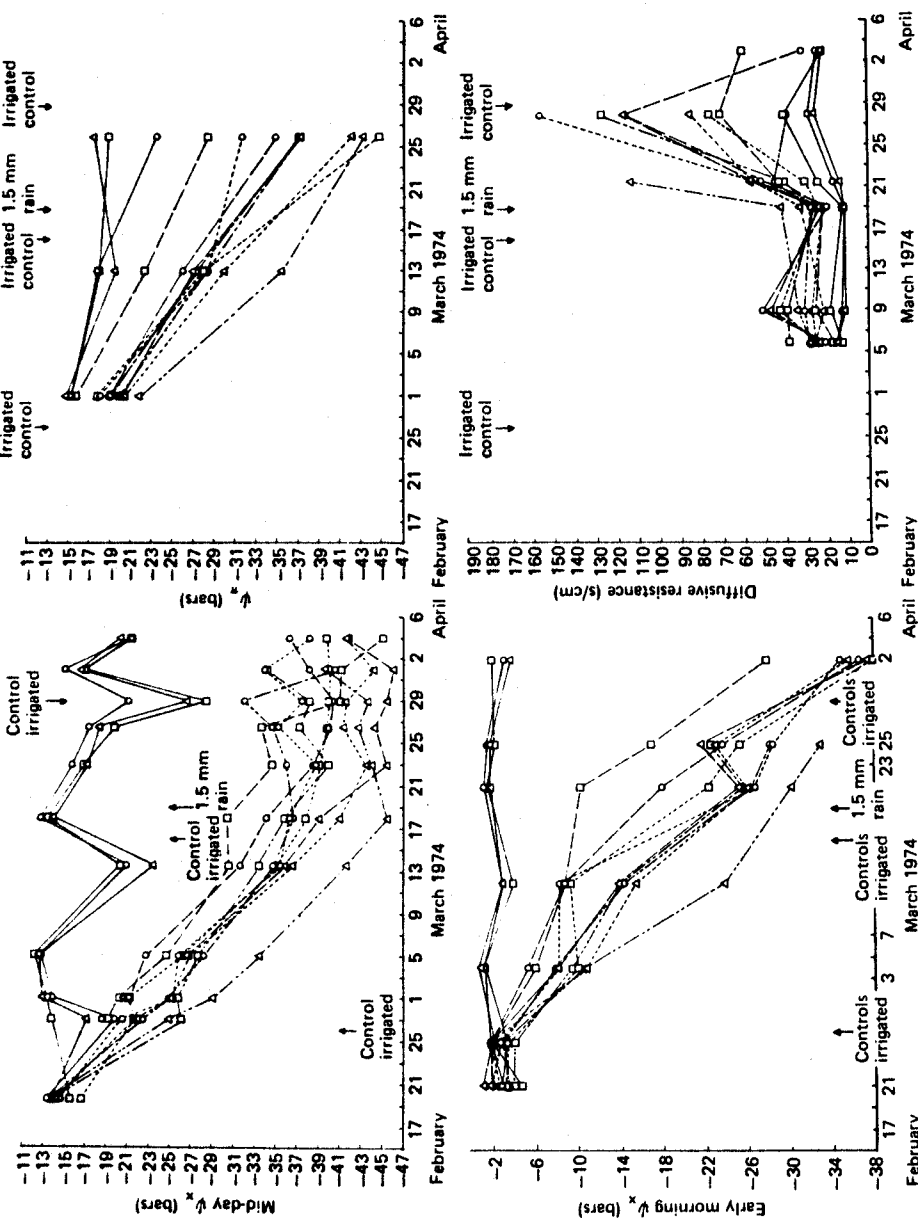


Figure 7.5 Seasonal time course of four plant-water stress components for three wheat genotypes. ○ Yecora; △ Cocorit;

cultivars being tested in the field are also too slow in themselves or are dependent on other slow measurement-components to be useful in field screening trials. Of course, in addition to plant and atmospheric stress measurements, determination of soil-water potentials and soil-water extraction are valuable environmental indices.

Significant strategic decisions must be made by the researcher to use these measurements effectively to characterize and compare properly stress response among cultivars. To assure the validity of their sampling procedures, Sojka, Stolzy and Fischer (1979, 1981) conducted numerous diurnal studies to identify time periods when crop-water status was stable over a sufficiently long interval to allow collection of large numbers of water-status measurements. They treated water-status parameters made during these intervals as though they were at steady state throughout the sampling period. Under their local conditions, an approximately six-hour period was statistically identified at midday when plant-water status parameters had zero slopes on diurnal response curves. In their preliminary work, they observed that rehydration from midday stress brought plant-water status as close to full recovery as it would achieve from the previous day's stress in one to two hours following sunset. Therefore, it was also feasible to compare the seasonal non-stressed equilibrium (or recovery) water status of each cultivar across the range of stress treatments imposed.

Figure 7.5 presents the previously unpublished 1974 seasonal time course of early-morning (before sunrise) ψ_x , midday ψ_x , midday ψ_{π} , and midday R_s for the three wheat genotypes (Yecora 70, Cocorit 71, and Gabo) studied intensively by Sojka, Stolzy and Fischer (1979, 1981). These data more fully characterize the seasonal stresses summarized in Figures 7.2 and 7.3. The consistency of the outlying responses of Cocorit 71 and Gabo across all four water-stress parameters is striking. At the time of their study, both Yecora 70 and Cocorit 71 were regarded as two of the best-available cultivars for production in the region where these experiments were conducted. In Figures 7.2 and 7.3 this is evident from the elevation of their response regressions above the population mean response (1:1 line). Particularly noteworthy about Cocorit was the sharp decrease in yield (especially in 1974) with stress. In examining Figure 7.5 it is apparent that in each parameter measured, Cocorit outlay the other two varieties toward the stressed end of the response scale. Yecora 70, which nearly parallels the mean in Figures 7.2 and 7.3, is between most of Cocorit 71's and Gabo's responses in Figure 7.5. Gabo, which shows a particularly drought-resistant yield response in Figure 7.2 for 1974, is usually in the low-stress range for all parameters in Figure 7.5.

Using Levitt's (1972) nomenclature, the relationship of each cultivar's water potential among treatments is an expression of its shift from stress avoidance into stress tolerance. Each cultivar's yield loss with falling water potential is an expression of its shift from strain avoidance to strain tolerance. The concept of conditioning (i.e. repair, or time-limited plastic response) is evident from the manner in which midday ψ_x ceases falling in Figure 7.5 for each treatment in the latter third of the observation period. A similar response was reported by Bidinger (1977) and by Fischer and Sanchez (1979).

Equally striking is how soon the pre-sunrise ψ_x fails to achieve full recovery after irrigation ceases. Equally important is the continuing decline in pre-sunrise ψ_x to the end of the observation period (even though midday ψ_x had stabilized). From the pre-sunrise ψ_x and diurnal ψ_x and R_s response, Sojka, Stolzy and Fischer (1979, 1980) concluded, as did Boyer and McPherson (1975), that on a daily basis there is only a brief period in the morning of vigorous photosynthesis and cell expansion in

stressed cereals. The limitation of these activities is therefore one of the most direct causes of reduced growth and yield during drought. This hypothesis would appear to be confirmed by the high correlation that Sojka, Stolzy and Fischer (1981) found for curvilinear regressions of yield on pre-dawn ψ_x (Figure 7.6) wherein yield loss had been almost fully expressed in the initial few increments of falling pre-dawn ψ_x . Fischer and Maurer (1978) also noted reduced sensitivity of yield to drought as the drought became more severe.

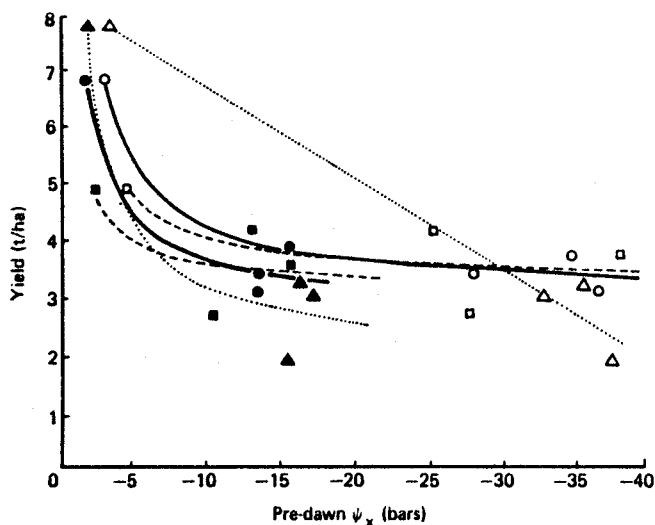


Figure 7.6 Sensitivity of yield in 1974 to predawn ψ_x . Best fit of Cocorit 71 low ψ_x in the form of $y = A + Bx$ was only slightly better than the form $y = A + (B/x)$ used for other plots. The r^2 for average ψ_x or low ψ_x fits were: 0.973 and 0.980, 0.948 and 0.975, and 0.516 and 0.572 for Yecora 70, Cocorit 71, and Gabo, respectively. Each point is the mean of four replicates. Average ψ_x : ●—● Yecora; ■—■ Gabo; ▲—▲ Cocorit. Low ψ_x : ○—○ Yecora; □—□ Gabo; △—△ Cocorit

Thorough interrelationships of a host of drought stress components including ψ_x , ψ_p , turgor pressure, relative water content, transpiration flux density, soil-water potential etc, have been reported by numerous groups (Bauer, 1972; Connor, 1975; Dedio, 1975; Biscoe, Cohen and Wallace, 1976; Jones, 1977b; Adjei and Kirkham, 1980; Bristow, DeJager and Van Zyl, 1981; Day, Lawlor and Legg, 1981). Others have interrelated photosynthesis with several of these parameters (Todd and Webster, 1965; Shimshi and Ephrat, 1975; Dedio, Stewart and Green, 1976). These relationships have been thoroughly and most recently reviewed for wheat by Kirkham and Kanemasu (1983).

While some success has been reported in discriminating cultivar response difference through R_s measurements (notably Shimshi and Ephrat, 1975), field measurements of R_s have generally proved to be more variable than those reported for controlled-environment studies. A number of papers have shown significant scatter in field-measured R_s for various reasons in a number of species in plant-water relations studies (Turner and Parlange, 1970; Sojka, Stolzy and Fischer, 1979, 1981; Jones, Pena and Carabaly, 1980; Squire and Black, 1981;

Kaufmann, 1982a,b; Sojka and Parsons, 1983). In addition, Sojka and Stolzy (1980) showed that R_s could be influenced by soil-oxygen diffusion rate and, in some instances, by soil temperature as well, in a number of species including wheat. Bell and Incoll (1981) and Bell and Squire (1981) showed 25–35% variation in R_s between porometers that they compared. A number of reviews and theoretical treatments of R_s porometry have identified problems in the development and application of theory (Berkowitz and Hopper, 1980; Hack, 1980; Chapman and Parker, 1981; Bristow, 1982). Several groups have reported that in most species stomatal closure does not occur gradually in response to stress. Instead, closure occurs abruptly upon reaching a stress threshold, and that these thresholds are affected by preconditioning and humidity (Raschke, 1975; Stange *et al.*, 1981; Turner and Begg, 1981). In view of these uncertainties associated with field R_s measurements, the peculiarities of stomatal function, and the stomatal abnormalities discussed in the previous section, the prospect for extensive use of porometry in field screening of large numbers of cultivars appears discouraging.

Many of the reviews already cited confirm the responsiveness of crops to atmospheric VPD. Burrows and Milthorpe (1976) argued that to best characterize plant-water status, LVPD (the difference between actual atmospheric vapor pressure and the saturated vapor pressure of air at the temperature of the leaf) rather than VPD should be used because it integrates internal plant-water status with the degree of externally applied stress.

A rapidly evolving new technology is arising around the non-contact sensing of canopy temperatures with infra-red thermometry. As transpiration takes place, the latent heat of vaporization results in cooling of the leaf by transpiration. As soil-water availability declines during drought periods, the conductivity of water through the soil-plant continuum also declines. As this occurs, water cannot be transported to the evaporative sites in leaves at a sufficient rate to meet the potential rate of evaporation. Surplus radiant energy then results in increased leaf temperature, often rising above atmospheric temperatures. Several strategies for using this concept to characterize stress have evolved. These include stress characterization simply as crop canopy temperature (T_c), canopy temperature minus air temperature (ΔT), the time integration of ΔT , which has been called the stress degree day (ΔTD), and the coupling of T_c with VPD and LVPD to determine a so-called normalized stress index (NSI) which is an attempt at rendering all IR-sensed canopy stress universally comparable for a specific crop regardless of the local soil and atmospheric conditions over the period of measurement (Jackson, Reginato and Idso, 1977; Ehrler *et al.*, 1978a,b; Idso *et al.*, 1981; Jackson *et al.*, 1981).

The technology and opportunities for using these techniques to select for drought resistance have already received some attention (Millard *et al.*, 1978; Blum, Mayer and Gozlan, 1982; Blum, 1983). Rapid stress assessment may be possible, perhaps more than once a day, and conceivably involving hundreds of varieties—or even thousands if over-flight IR photography or radiometry can be adapted. The technology may be restricted to clear dry physiographic regions, however, and to exacting cultural and sampling protocol. Variation in incoming radiation caused by haziness or clouds, plant age, canopy coverage, canopy geometry, and possibly relative humidity have all been identified as sources of variation affecting several aspects of IR sensing and the relationships of the factors composing the NSI (Idso and Jackson, 1968; Heilman, Heilman and Moore, 1981; Geiser *et al.*, 1982; Idso, 1982; Sojka *et al.*, 1984).

Progress and prospects: a commentary

Drought-resistance research has had a history much like the story of 'the little engine that could'. Three or four decades ago, few held out hope for significant progress in breeding for drought resistance. Like the little engine, however, seeing the great need inspired a commitment. A running start was made at the hill, solving the more obvious and easier problems first. To reach the top, however, an effort must be made to sustain the momentum. I think we can ... I think we can.

To be successful will require a redoubling of effort in some areas and a movement away from others to new thrusts. Basic plant-water relations research may have reached a plateau of understanding in some areas. Much of our current research is contributing less new knowledge than some of us may care to admit. Where water-relations research dovetails with drought-resistance breeding, there are several arenas that have barely been identified to date, let alone explored. Below are some examples.

In 1964 Allard and Bradshaw pointed out that individual response and population responses to stress can be quite different, because of the genetic diversity of populations. They called this phenomenon 'population buffering'. These principles have not been studied with any commitment in grain-crop production or at a sufficient level of sophistication to date. It is highly likely that varying 'mixes' of cultivars (i.e. literally mixed seed) could have profoundly different responses to drought than the proportional sum of the single cultivars. The principle is an established one in range science. Both the combinations of cultivars and their relative proportions in mixtures deserve a closer look. A similar argument might be made for an extensive effort of drought evaluation of hybrid seed and perhaps even hybrid mixtures.

Root-diameter reduction of as much as 25% has been reported by several authors in association with decreased ψ_x (Huck, Klepper and Taylor, 1970; Cole and Alston, 1974; Tinker, 1976; Faiz and Weatherly, 1978). Contraction of roots separates much of their surface area from the water-films surrounding soil particles, increasing the effective resistance for water entry. There has been no effort of which the author is aware, to screen for less elastic root systems.

Similarly, while it has long been known that mycorrhizal associations form on the surfaces of cereal roots, little or no work has been undertaken to determine if field inoculation with mycorrhiza is feasible, if mycorrhiza have a significant impact on plant-water relations, or if mycorrhizal strain \times cultivar interactions are specific, thus requiring testing for optimal strain \times cultivar combinations.

An important production strategy for achieving drought resistance is to promote early deep rooting. There is insufficient information on the interaction of various production and cultural practices with cereal cultivars for maximum root expression. A major factor which limits early plant development and root growth is the impact of soil and shoot temperatures on plant growth. Numerous studies have been conducted on the effect of reflectants and anti-transpirants sprayed on crops to lower temperatures and reduce transpiration in established crops. No work has been undertaken to increase the radiation absorbancy of early crop canopies or of light-colored soils to promote early stand establishment and root growth through increased heat retention. This goal might be achieved by dusting with fine carbon powder, or by mixing dyes with herbicides, fungicides, or the like. Individual cultivars would, in all likelihood, display differences in response to these treatments. Root/shoot ratios of soybean have been shown to be greatly affected by

the spectral quality of light to which shoots are exposed (M.J. Kasperbauer, personal communication). There may be inert or non-toxic dyes or other surface coatings which could be sprayed on developing canopies that would filter incoming radiation to enrich the desired spectral segment, thereby increasing the root-to-shoot ratio. Again, this response is likely to be different among cereal cultivars.

Summary

Although a single comprehensive physiological definition of drought resistance may not exist, two points regarding identification of drought resistance bear repeating. There is a difference between assays for the presence of traits associated with drought resistance and tests that prove a cultivar is drought resistant. Secondly, drought resistance can be determined only by determining a crop's actual yield, in the field, as a function of some quantifiable index of stress severity.

Although Blum (1983) noted a general lack of information on the relationships between physiological adaptive traits and yield, precise morpho-physiological characterizations are of limited value to the breeders if they are not quantitatively tied to a field-derived, stress-indexed measurement of yield. Conversely, precise yield comparisons associated with non-quantifiable indices of stress contribute little. In addition, in all likelihood, there are a number of quantitative stress indices that can be used in characterizing drought resistance. The specific nature of these inputs will depend upon the particular needs of each specific breeding program.

Finally, as always, and as in all scientific endeavors, there is a constant and urgent need to think creatively and explore untried approaches, even if they go against the momentary conventional wisdom. Progress has never come in any other way.

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